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Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species

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Summary

1. Predictions of the identities and ecological impacts of invasive alien species are critical for risk assessment, but presently we lack universal and standardized metrics that reliably predict the likelihood and degree of impact of such invaders (i.e. measurable changes in populations of affected species). This need is especially pressing for emerging and potential future invaders that have no invasion history. Such a metric would also ideally apply across diverse taxonomic and trophic groups.

2. We derive a new metric of invader ecological impact that blends: (i) the classic Functional Response (FR; consumer *per capita* effect) and Numerical Response (NR; consumer population response) approaches to determining consumer impact, that is, the Total Response (TR = FR × NR), with; (ii) the 'Parker–Lonsdale equation' for invader impact, where Impact = Range × Abundance × Effect (*per capita* effect), into; (iii) a new metric, Relative Impact Potential (RIP), where RIP = FR × Abundance. The RIP metric is an invader/native ratio, where values >1 predict that invader ecological impact will occur, and increasing values above 1 indicate increasing impact. In addition, the invader/invader RIP ratio allows comparisons of the ecological impacts of different invaders.

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3. Across a diverse range of trophic and taxonomic groups, including predators, herbivores, animals and plants (22 invader/native systems with 47 individual comparisons), high-impact invaders were significantly associated with higher FRs compared to native trophic analogues. However, the RIP metric substantially improves this association, with 100% predictive power of high-impact invaders.
4. Further, RIP scores were significantly and positively correlated with two independent ecological impact scores for invaders, allowing prediction of the degree of impact of invasive alien species with the RIP metric. Finally, invader/invader RIP scores were also successful in identifying and associating with higher impacting invasive alien species.
5. *Synthesis and applications*. The Relative Impact Potential metric combines the *per capita* effects of invaders with their abundances, relative to trophically analogous natives, and is successful in predicting the likelihood and degree of ecological impact caused by invasive alien species. As the metric constitutes readily measurable features of individuals, populations and species across abiotic and biotic context-dependencies, even emerging and potential future invasive alien species can be assessed. The Relative Impact Potential metric can be rapidly utilized by scientists and practitioners and could inform policy and management of invasive alien species across diverse taxonomic and trophic groups.

Key-words: ecological impacts, functional response, invasive alien species, maximum feeding rate, numerical response, prediction, relative impact potential metric, risk assessment, species abundance, taxonomic and trophic groups

Introduction

In recent decades, invasion ecology has advanced substantially in providing understanding of the ecological impacts of invasive alien species, here defined as measurable changes in populations of affected species (see Ricciardi & Cohen 2007; Simberloff *et al*. 2013; Caffrey *et al*. 2014; Jeschke *et al*. 2014; Kumschick *et al*. 2015). For example, introduced predators can drastically impact populations and communities of native prey species (e.g. Salo *et al*. 2007; Wanless *et al*. 2007; Dick, Alexander & MacNeil 2013a; Dick *et al*. 2013b). However, beyond broad generalizations such as these, the search for species traits (e.g. body size, fecundity, behaviour) that reliably predict invasion success and ecological impact has generally failed (Parker *et al*. 2013; Dick *et al*. 2014). This has also hindered those who require better risk assessments for invaders since, although invasion history can inform likely future impacts of an invader (Kulhanek, Ricciardi & Leung 2011; Ricciardi *et al*. 2013; Blackburn *et al*. 2014), there is currently no way of predicting the ecological impacts of emerging and future potential invaders that have no invasion history.

IUCN Aichi targets state that, by 2020, 'invasive alien species and pathways are identified and prioritized, that priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment'. Additionally, recent EU IAS legislation (EU Regulation 1143/2014) required member states to develop a list of invasive alien species of EU concern (see EU 2016/1141). Key criteria for listing such species are ostensibly based on 'available scientific evidence' and that the species is 'likely to have a significant adverse impact on biodiversity or the related ecosystem services'. These lists are dynamic at the Member State and EU levels and hence there is an urgent need to identify and prioritize IAS of regional and indeed global concern. However, while we have impact measures and classifications for established invaders (e.g. Blackburn *et al*. 2014; Laverty *et al*. 2015b), there is currently no way of predicting the impact of new invaders. While horizon scanning has a good record in predicting new and damaging arrivals (Roy *et al*. 2014), and such exercises are often based on 'expert opinion' coupled with best available evidence (see Blackburn *et al*. 2014), we still need a quantitative methodology to rapidly assess potential impacts of invaders that can be applied by stakeholders and practitioners.

Comparative analyses of invader and native Functional Responses (FRs; Fig. 1a) have recently been identified as a useful means of identifying high-impact invasive alien species (Dick *et al*. 2014). FRs define the relationship between resource availability (e.g. prey density) and consumer uptake (e.g. prey consumption rate). For example, the well-known ecologically damaging bloody red shrimp *Hemimysis anomala* Sars 1907 has a higher maximum feeding rate (the asymptote of the FR) than its native ecological equivalent species *Mysis salemaai* Audzijonyte & Vainola 2005 (Dick *et al*. 2013b) and this difference correlates with degree of field invader impact on different prey species (Fig. 1b–d).

Classically, the FR describes the *per capita* effect of a predator (or other consumer) on prey (or other resource) as the density of prey (resource) increases, with the

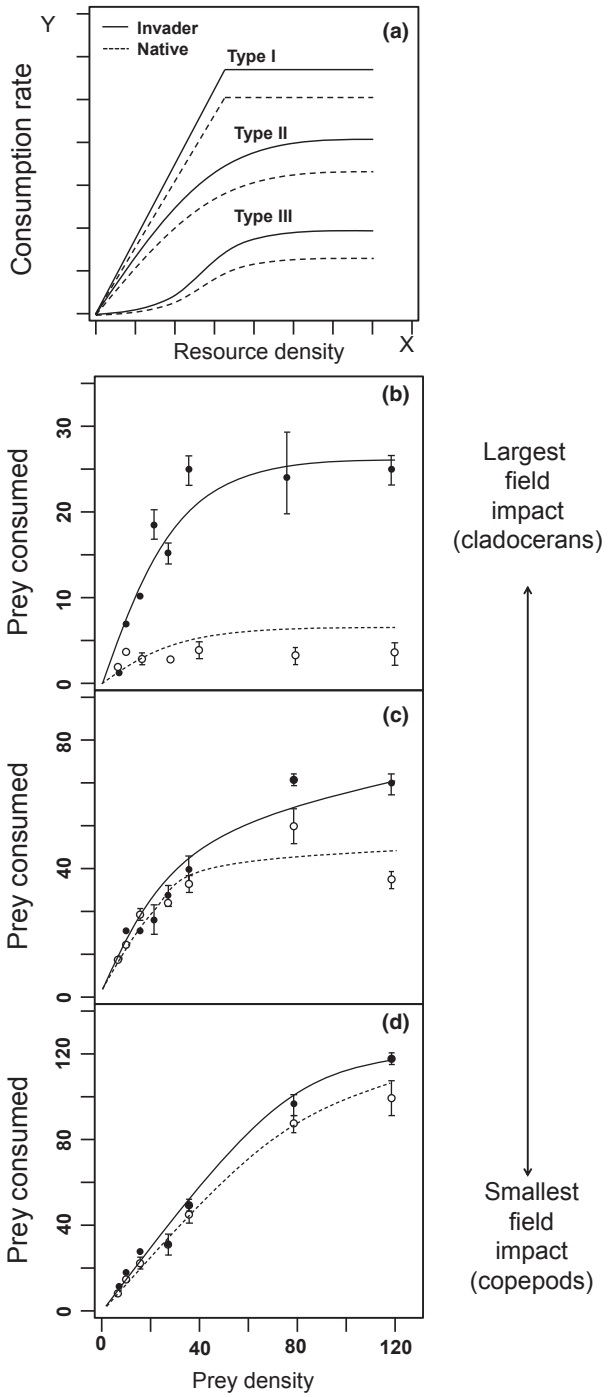

Fig. 1. (a) Functional response (FR) types and hypothetical invader/native comparisons; (b–d) differences in FRs between an invasive mysid shrimp (*Hemimysis anomala*, closed circles, solid line) and a native comparator (*Mysis salemaai*, open circles, dashed line) explains and predicts known field impacts of the invader on zooplankton prey species (b and c = cladocerans, d = copepods; redrawn from Dick *et al*. 2013b).

reciprocal of the 'handling time' parameter h giving the estimated maximum feeding rate (curve asymptote). The Numerical Response (NR) describes the predator population response as the density of prey increases (NR = both predator aggregation and predator reproduction; Solomon 1949; Holling 1959a,b). The overall effect on the prey population, the 'Total Response' (TR), is then the product of the FR and the NR, that is:

$$TR = FR \times NR \quad \text{eqn 1}$$

Similarly, invasion ecologists (Parker *et al*. 1999; the 'Parker–Lonsdale equation') recognized that the Impact (I) of an invasive alien species on a native resource (e.g. predator on prey) could be quantified as the product of the Range (R) of the invasive alien species, its Abundance (A) and *per capita* effect (E), that is:

$$I = R \times A \times E \quad \text{eqn 2}$$

When considering trophic interactions of an invader with a resource, the Parker–Lonsdale equation is essentially the TR equation with the addition of Range, reflecting the assumption that a native species exists throughout its 'natural' range, whereas invasive alien species are, by definition, increasing their range from an initial absence. However, *per capita* effects were never expressed as FRs by Parker *et al*. (1999) or subsequent invasion ecologists (see Dick *et al*. 2014), nor was the Numerical or TR terminology utilized. The realization that the Parker–Lonsdale equation and the classic TR equation were essentially equivalent led Dick *et al*. (2014) to suggest the use of FRs as a *per capita* measure of invader impact, in particular comparing the FRs of invaders with trophically analogous natives, to understand and predict invader impacts. This approach has been generally successful, with many high-impact invaders showing significantly higher FRs than native species as well as non-impacting introduced species (Fig. 1b–d; see also Alexander *et al*. 2014; Laverty *et al*. 2015a; Xu *et al*. 2016). However, as discussed by Dick *et al*. (2014), the full potential of an invader in its impact on native prey populations may be better described as the product of the FR and NR. However, unlike FRs, which are often readily measured, the NR is a more nebulous and difficult measure (e.g. due to time lags). We suggest, however, that this could be simply replaced with the proxy of consumer abundance, which captures aggregation, reproduction and the long-term net effect of resources assimilated into consumers. Such abundance data may already be available for the species in question, particularly as a result of routine monitoring programmes, or can be easily estimated in the field when required. In the absence of existing invasions, reasonable if slightly conservative estimates of invader densities could be obtained from populations in the native range (see Hansen *et al*. 2013; Parker *et al*. 2013).

In this paper, we present a new metric that blends facets of eqns 1 and 2 above, to predict invasive alien species impacts. We then explore the utility of the metric in predicting the identities of ecologically damaging invasive alien species, and the likelihood and degree of their ecological impacts by quantifying the relationship between

established scores of ecological impact and our novel predictive metric. We propose that our new metric has much potential utility for scientists, managers, practitioners and policy makers who are often tasked with intervention ecology (Hobbs *et al*. 2011) and the associated cost-benefit analysis involved in invasive species management and control.

Methods and Results

We propose a new metric for the ecological impact of invasive alien species, the Relative Impact Potential (RIP) metric, as the product of the consumer FR and a measure of consumer ABundance (AB). Firstly, the Impact Potential (IP) can be derived for any species as:

$$\mathrm{IP} = \mathrm{FR} \times \mathrm{AB} \qquad \text{eqn 3}$$

However, this only gives an absolute IP value that has no meaning relative to the baseline, that is, the existing impact of the native analogous consumer species (or put another way, a baseline consumer-resource co-evolutionary relationship). Thus, as with our comparative FR approach, that compares the FRs of invaders with the FRs of natives (see Dick *et al*. 2014), we propose that the IP of invaders becomes relative to the IP of natives, such that the RIP is:

$$\mathrm{RIP} = \left(\frac{\mathrm{FRinvader}}{\mathrm{FRnative}}\right) \times \left(\frac{\mathrm{ABinvader}}{\mathrm{ABnative}}\right) \qquad \text{eqn 4}$$

where FR = the estimated maximum feeding rate from the FR curves (i.e. curve asymptotes) and AB = the field abundance/density (or biomass; see below) of the species. Thus, when RIP < 1, the invader is predicted to have less impact than the native equivalent(s); when RIP = 1, we predict no impact above that driven by native equivalents; whereas RIP > 1 indicates likely invader ecological impact. As an example (see also Table S1, Supporting Information), we have FRs for the invasive freshwater amphipod *Gammarus pulex* (Linnaeus 1758) and the native analogue *Gammarus duebeni celticus* Stock & Pinkster 1970 (which is replaced by the invader) towards two prey species, mayfly nymphs (*Baetis rhodani* Pictet 1844) and blackfly larvae (*Simuliidae* spp.) (Laverty *et al*. 2015a). Further, we have ABs from Kelly *et al*. (2003, 2006) of *G. pulex* and *G. d. celticus* at two contiguous sites in the River Lissan, N. Ireland, where one site contains only *G. pulex* (a long-term invaded site) and the other site only *G. d. celticus*, and where environmental variables were consistent between sites, giving:

$$\mathrm{RIP} = \left(\frac{17{\cdot}76}{12{\cdot}96}\right) \times \left(\frac{136}{17}\right) = 10{\cdot}96 \text{ for mayfly larvae prey,}$$

and

$$\mathrm{RIP} = \left(\frac{17{\cdot}98}{10{\cdot}32}\right) \times \left(\frac{136}{17}\right) = 13{\cdot}94 \text{ for blackfly larvae prey.}$$

These RIP values of well above 1 corroborate with dramatic declines in both *B. rhodani* and *Simuliidae* spp. following invasion by *G. pulex*, and its replacement of the native *G. d. celticus*; indeed, the invader causes widespread declines in macroinvertebrate species richness, diversity, abundance and biomass (Kelly *et al*. 2003, 2006).

However, depending on the data available, either single estimates of FR and AB (as above), or means and standard errors [or variance, standard deviations (SDs), CIs] or a mixture, will be available, and hence we can often incorporate variation and uncertainty into the RIP metric. To do this, we make the assumption that the observed FR and AB measures are samples from underlying distributions of values. Because both measures are strictly positive we use a simple log-normal form for both underlying distributions. Our goal here is the probability density function (pdf) for the RIP measure given the four input pdfs (two numerators, two denominators). It is possible to do this by repeated sampling from the four pdfs, calculating the RIP each time, and repeating until a smooth distribution of RIP values is obtained. Fortunately, there exists a shortcut in that if we know the means and SDs of the four pdfs, the output pdf for RIP is available explicitly in mathematical form using these means and SDs (see R script in Appendix S1). Thus, eqn 4 can often become:

$$f(\mathrm{RIP}) = \left(\frac{f(\mathrm{FRinvader})}{f(\mathrm{FRnative})}\right) \times \left(\frac{f(\mathrm{ABinvader})}{f(\mathrm{ABnative})}\right) \qquad \text{eqn 5}$$

where $f()$ indicates the pdf.

We then use the pdf $f(\mathrm{RIP})$ and report mean RIP and the confidence intervals (80% and 60%) and the probability that mean RIP is greater than 1, or any other figure (e.g. >10; see Table S1). Thus, using means and SDs from the first worked example above [i.e. mean (SD) = 17·76 (7·9); 136 (50); 12·96 (3·2); 17 (15)], we get:

$$\mathrm{RIP} = 20{\cdot}68 \begin{pmatrix} 80\%\ \mathrm{CI} = 3{\cdot}72 - 44{\cdot}8 \\ 60\%\ \mathrm{CI} = 5{\cdot}7 - 16{\cdot}25 \\ P_{\mathrm{RIP}} > 1 = 99{\cdot}6\% \\ P_{\mathrm{RIP}} > 10 = 60{\cdot}3\% \end{pmatrix}$$

The RIP metric has great potential to significantly enhance the reliability of predictions of invader ecological impact because, while FR alone is often useful in impact prediction, there may be cases where the *per capita* effect of a damaging invader is low, but the RIP is high because of high invader relative to native species abundance. Also, there may be cases where damaging invasive alien species are not numerous compared to natives, but exert high impact through relatively high *per capita* effects. All such permutations of *per capita* and abundance aspects of invasive alien species can thus be captured in the RIP metric.

Table S1 presents all invader/native FR comparisons conducted by the present authors and from the literature to date (see review and search terms in Dick *et al*. 2014). All are study systems where the invader is known to have a measurable degree of negative ecological impact (see Table S1). Across the 22 independent systems (defined as each distinct invader species/native species comparison) in Table S1, the FR of the ecologically damaging invader was higher than the FR of the native analogue in 18/22 cases (χ^2 goodness–of-fit test = 8·9, d.f. = 1, $P = 0{\cdot}003$), whereas RIP was greater than 1 for all 22/22 cases ($\chi^2 = 22$, d.f. = 1, $P < 0{\cdot}001$, $P = 2{\cdot}7 \times 10^{-6}$). Considering all FR comparisons in Table S1 (i.e. even where there were multiple FR comparisons within systems, such as more than one prey species tested), we found that FRs predicted impact in 39/47 cases ($\chi^2 = 20{\cdot}45$, d.f. = 1, $P < 0{\cdot}001$, $P = 6{\cdot}1 \times 10^{-6}$), but RIP was

greater than 1 for all 47/47 cases ($\chi^2 = 47$, d.f. = 1, $P < 0{\cdot}001$, $P = 7{\cdot}1 \times 10^{-12}$). Further, there were significant positive relationships between our RIP metric and the independent Ecological Impact Scores of Laverty *et al.* (2015b) and Ricciardi & Cohen (2007) (Table 1; Fig. 2a and b; see also Appendix S2; Fig. 2a, $F_{1,10} = 23{\cdot}5$, $P < 0{\cdot}001$; Fig. 2b, $F_{1,10} = 15{\cdot}1$, $P < 0{\cdot}005$).

Table S1 also presents a small number ($n = 7$) of invader/invader comparisons, where the more ecologically damaging of two invasive alien species were in all cases predictable from both their FR and RIP metrics.

Discussion

The use of FR metrics to predict invader impact has, to date, largely examined only this *per capita* impact of individuals, with little consideration of impact through population-based NRs or other consumer abundance measures (Dick *et al.* 2014; Table S1 here). Such studies have, however, often been well reconciled with observed field impacts, where higher FRs of invaders compared to native trophic analogues are associated with declines in, for example, native prey and plant species (e.g. Dick *et al.* 2013b; Alexander *et al.* 2014; Dodd *et al.* 2014; Xu *et al.* 2016). In this study, we found a significant association between higher invader than native FRs and ecological impacts, with >80% of systems comparisons following this pattern. FRs could be inherently more important than NRs in determining ecological impact because, for example, highly efficient predator individuals can have devastating impacts on prey populations (e.g. individual foxes preying on turtle nests in Australia; Spencer, Van Dyke & Thompson 2016). Additionally, FRs might be correlated with NRs, and hence the former measure has inherently high predictive power in terms of ecological impact (Dick *et al.* 2013b, 2014). However, a major advance in invader impact prediction was revealed in this study when a proxy for NRs, the field abundances of invaders/natives, was incorporated into our RIP metric. This is a blend of the classic TR equation (TR = FR × NR) and the Parker *et al.* (1999) invader equation [Impact = Range × Abundance × Effect (*per capita*)]. Our RIP metric had 100% success in associating with high-impact invasive alien species using available studies (Table S1).

We also found the RIP metric correlates significantly and positively with other independent measures of invader ecological impact, these being the scoring systems of Laverty *et al.* (2015b) and Ricciardi & Cohen (2007). RIP thus gives excellent predictive power as to both the likelihood and magnitude of invader ecological impact, and also provides a mechanistic understanding of why some invaders have their degree of ecological impact. This metric could also facilitate the assessment of emerging and potential future invader identity and likely impact. For example, following Ricciardi & Rasmussen (1998), existing/emerging dominant vectors and their connected donor

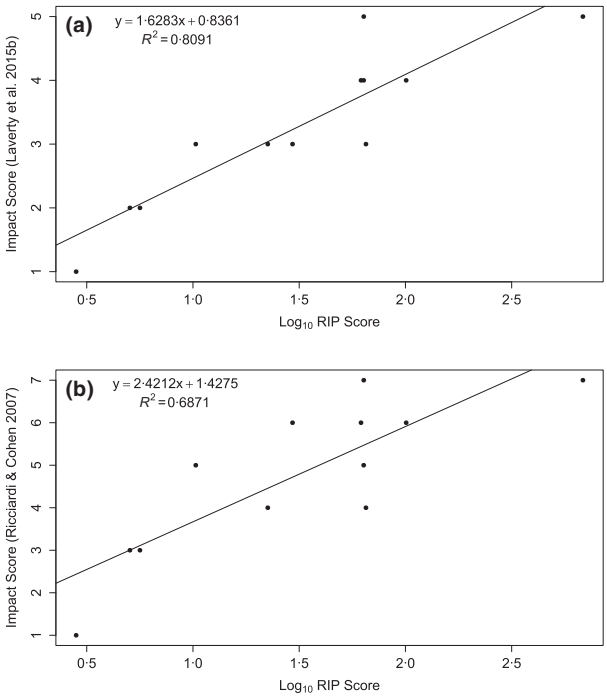

Fig. 2. Least-squares linear regressions of Ecological Impact Scores against $\log_{10}$ Relative Impact Potential scores (Method 2 eqn 5; see also Table S1 and Table 1 and Appendix S2), for (a) scores from Laverty *et al.* (2015b) and (b) Ricciardi & Cohen (2007).

Table 1. Ecological Impact Scores from Laverty *et al.* (2015b) and Ricciardi & Cohen (2007), and $\log_{10}$ Relative Impact Potential (RIP) scores (this study; ordered highest to lowest RIP; Method 2, eqn 5, Table S1). Laverty *et al.* (2015b) and Ricciardi & Cohen (2007) are ordinal rankings of categories of impact, based on measurable negative impacts on native species populations and include a category of 0 for no demonstrable impact. Where an invasive alien species had multiple RIP scores (e.g. across several prey species; see Table S1) we took the mean RIP score (Method 2, eqn 5; see Table S1) for Table 1 and Figure 2a and b. See also Appendix S2. We only present these analyses for systems where the invader is known to exhibit impact on the resource in question (e.g. predator impacts on prey), and not examples where impact is more diffuse with no direct impacts on the resource in question (e.g. gamba grass impacts fire regime, but not nutrients directly; see Table S1)

Invasive Alien Species	Laverty *et al.* (2015b) score	Ricciardi & Cohen (2007) score	$\log_{10}$ RIP score
Neogobius melanostomus	5	7	2·83
Hemimysis anomala	4	6	2·1
Pomacea canaliculata	3	4	1·91
Clarias gariepinus	4	5	1·8
Dikerogammarus villosus	4	6	1·79
Pseudorasbora parva	5	7	1·49
Gammarus pulex	3	6	1·47
Micropterus salmoides	3	4	1·35
Harmonia axyridis	3	5	1·01
Pacifastacus leniusculus	2	3	0·71
Lepomis macrochirus	2	3	0·7
Eriocheir sinensis	1	1	0·45

pools could be used as a guide to assess possible future invaders. The RIP method is also a readily available tool for practitioners, with relatively simple calculations (see also Supporting Information). For example, this approach could be applied to existing and potential new candidates for the EU lists of invasive alien species of Union and regional concern (EU Regulation 1143/2104), for invasive alien species 'horizon scanning' exercises (e.g. Gallardo & Aldridge 2013; Caffrey *et al.* 2014; Roy *et al.* 2014) and incorporated into existing invader impact classification frameworks (e.g. Blackburn *et al.* 2014).

The data sets of Table S1 are clearly biased towards high-impact invasive alien species, as these have received the most attention from scientists and practitioners. To fully test the utility of FRs and RIP, we require studies of low impact/benign introduced species, which should return RIP values of around or <1. This would enhance both our understanding of invader impact and add confidence to the RIP metric as able to recognize and assess both damaging and more benign alien species. In addition, the RIP method requires native comparators and, while this has not been a problem thus far (see Table S1), there may be times when there are multiple candidates, or indeed none. In the former scenario, the invader/native RIP can be calculated for each comparator, and individual and overall RIP values derived. In the latter scenario, if there happens to be no native analogue (e.g. with mammalian predators introduced to islands), then that alone should signal a high risk potential as functionally distinctive invaders are often the most ecologically damaging (see Ricciardi & Atkinson 2004). Further, RIP can compare among multiple invaders (see Table S1) to predict which will have the higher impact and hence should attract most preventative action.

The RIP metric is clearly influenced by predator (or other consumer) abundance estimates (and SDs) used in its calculation, but we found collation of these data remarkably difficult (see also Parker *et al.* 2013). While we acknowledge that abundances of both invaders and natives are highly variable (see also Hansen *et al.* 2013) and subject to myriad influences (particularly season and spatial heterogeneity of habitat), with lag times in population growth, we did manage to compile comparative abundance data for each system that controlled (to various degrees) for abiotic/biotic confounds. Also, however, the abundance estimates that we use incorporate both aggregative and reproductive elements that are often separated in the consideration of NRs. Thus, for example, abundances of invasive *G. pulex* and its native analogue *G. d. celticus* were derived from contiguous stretches of the same river where physicochemical influences for both species were similar. Hence, we assume their abundances in the RIP calculation reflect true differences in invader/native species abundances, all else being equal. We recommend that future RIP calculations incorporate abundance estimates that avoid confounds of differing environmental and biological factors; however, our method is sufficiently robust with imperfect data, and such context-dependencies can also be explicitly incorporated and addressed in invader impact prediction with RIP. In addition, where abundance/density comparisons among invaders and natives make little sense (e.g. when invaders are relatively massive in size, but scarce in numbers), then biomass may be a better element of RIP; for example, the invasive sharptooth catfish (*Clarias gariepinus* Burchell 1822) vs. native river goby (*Glossogobius callidus* Smith 1937) example in Table S1 (system 19). Finally, as invaders may initially add to the existing ecological impact of native analogues, and later in the invasion process either partially or completely replace such natives, then consideration of RIP throughout the replacement process may further elucidate spatiotemporal patterns of invader impact, and we encourage further research in this area.

The *per capita* feeding rate of an invader may be reduced by its own and other species' abundances through mutual interference, cannibalism and intra-guild predation (e.g. see Médoc, Spataro & Arditi 2013). In other cases, multiple predator impacts may be simply additive (e.g. Barrios-O'Neill *et al.* 2014) or synergistic (Pintor, Sih & Kerby 2009; Zimmermann *et al.* 2015). Alterations of predator behaviour are collectively termed 'multiple predator effects' (Sih, Englund & Wooster 1998), and these clearly may alter predictions of RIP. However, the FR of groups as opposed to single individuals can be measured and incorporated into RIP calculations. In addition, this study shows that this level of complexity may not be required for rapid and effective usage by practitioners, since the RIP scores presented here, based on the FRs of single individuals, are reliable predictors of impact across invader systems. FRs also lend themselves to measurement under other specific context-dependencies, both biotic (e.g. Barrios-O'Neill *et al.* 2015, 2016) and abiotic (e.g. Laverty *et al.* 2015a), such that RIP can also be modified in its calculation and use. For example, RIP assessments conducted under differing temperatures may be used to predict ecological consequences of invasive alien species under climate change scenarios (see use of FRs in this context; Iacarella *et al.* 2015).

Prey naïveté and functional distinctiveness of predators are prominent features of invasion scenarios (Rehage, Dunlop & Loftus 2009). Prey recognize predators *via* chemical, visual or auditory cues (Abbott 2006; Gherardi *et al.* 2011; Carthey & Banks 2014); therefore, experience and co-evolutionary history are prerequisites for prey to react appropriately to a predator (Cox & Lima 2006). The 'naïve prey' hypothesis posits that prey without prior experience of an invasive predator may incur greater mortality than that with a native predator, as the anti-predator response is inappropriate or absent (Diamond & Case 1986; Banks & Dickman 2007; Sih *et al.* 2010). Prey naïveté has been observed across taxa including mammals, birds and fish (McLean, Barbee & Swearer 2007; Salo *et al.* 2007; Edgell & Neufeld 2008; Barrio *et al.* 2010; Fey *et al.* 2010; Paolucci, MacIsaac & Ricciardi 2013),

indicating that it is a pervasive feature increasing invader impact on recipient systems. Partitioning the effects on the FR of predator novelty (e.g. with respect to weaponry, speed of attack) and prey naïveté is important as, for example, naïveté may decline in a prey population over time (Gérard *et al*. 2014), leading to changes in *per capita* effects and overall impact. Again, the RIP metric can capture and predict such effects by, for example, examining the FRs of individuals at different spatiotemporal stages of invasion and individuals that vary in the archetype of enemies encountered.

Body size underpins the feeding rates of consumers (e.g. Woodward & Hildrew 2002; Woodward *et al*. 2005). In general, smaller consumers exhibit lower *per capita* rates of resource acquisition than do larger consumers, as typified by lower attack rates and longer handling times (Rall *et al*. 2012). At the same time, smaller consumers are almost inevitably more abundant (Cohen, Jonsson & Carpenter 2003; Woodward *et al*. 2005). In the context of understanding the RIP of invasive alien species, these empirically well-founded patterns have two corollaries: (i) that smaller consumers may exert higher population-level impacts on a mutual resource exploited by larger species, despite lower *per capita* feeding rates and; (ii) that the reciprocal is true where larger, less abundant consumers have very high *per capita* feeding rates. The current RIP metric captures much of this with its balance between the relative FR and relative population abundances (or biomasses) of invaders and natives. For example, the invasive mysid shrimp, *H. anomala*, is smaller than its native counterparts and therefore expectations are of higher abundances and lower *per capita* feeding rates, but empirical evidence suggests that the *per capita* feeding rates of the invader are in fact much higher than those of the larger native (Dick *et al*. 2013b; Barrios-O'Neill *et al*. 2014; Table S1). Conversely, the invasive gammarid shrimp, *Dikerogammarus villosus* Sowinsky 1894 is typically larger than the native counterparts it displaces, yet even size-matched FR trials reveal higher feeding rates for this species, while larger individuals are increasingly voracious (Dodd *et al*. 2014; Table S1; see also Xu *et al*. 2016). *D. villosus* is thus larger, has higher inherent *per capita* feeding rates and can be more abundant (see Table S1) than native counterparts. A further potential complication for RIP is ontogenetic shifts in resource use, such that invader/native FR/RIP comparisons across body size may be further confounded. This can be remedied by appropriate studies, such as that of Dick, Alexander & MacNeil (2013a), who showed that an invader amphipod was in fact predatory throughout its life history. In each case, provided species are trophically analogous consumers of mutual resources, the RIP framework offers a succinct, tractable means of rapidly assessing possible invader impacts, even where considerable differences in consumer size (and biomass) exist.

A further important element of FR derivation and subsequent RIP calculations is the choice of prey/resource that is presented to the consumers. At one extreme, the prey can be ecologically relevant, that is, actual prey species encountered in the field by the invaders and native analogues. This allows direct matching of FR/RIP and impact in the field. For example, with invasive *H. anomala*, smaller invader/native differences in FR/RIP are associated with prey species less affected in actuality (Dick *et al*. 2013b). At the other extreme, the prey species may be a general item used to reveal overall FR differences between invader and native. For example, Alexander *et al*. (2014) used tadpoles as a proxy of the myriad vertebrate and invertebrate prey of invasive/native fish in South Africa, revealing inherently higher FRs in damaging invaders compared to natives, which corroborated with field impacts (see also Table S1 here). We also stress that the impact of the invader may not always be on the resource in question, and that high FRs and RIPs may be characteristic of high-impact invasive species generally. For example, gamba grass (see Table S1) has impact through changing fire regimes, but its identification as a high-impact invader is still evident in our FR and RIP methodology.

Finally, we have drawn on studies across a diverse range of taxonomic and trophic groups (see Table S1), including invasive crustaceans, molluscs, insects, plants and fish, with animal trophic groups ranging from predators to herbivores and filter feeders. Since all organisms utilize resources, there is no reason that FRs cannot be derived for any invader, either experimentally or from surveys and other methods (see Dick *et al*. 2014). Coupled with abundance/biomass estimates and straightforward RIP calculations (see Table S1 and other Supporting Information), the metric is applicable to any invasion scenario. Indeed, we have demonstrated that the metric may be useful in comparing two or more invaders, such that the increasing scenario of temporal sequences of invasions by new species can be assessed for likely ecological impacts (see also Jackson 2015).

In summary, despite a number of issues that can complicate its derivation, our RIP metric encapsulates differences in FRs and abundances between invaders and natives and provides a tool to assess which species are likely to have ecological impact and what that degree of impact might be. Complexities and context-dependencies affecting both FRs and abundances can be incorporated into the RIP metric if desired; the technique also provides a mechanistic explanation for invader ecological impact. Most of all, however, we propose RIP as a simple and rapid, yet apparently powerful, predictive tool for scientists and practitioners that can inform invasive alien species risk assessments, interventions, policy and legislation.

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Data accessibility

All data used in this study are contained within Table S1.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Method 1 and 2 regression plots for (a) eqns 4 and (b) 5.

Fig. S2. Method 1 eqn 5 regression plots for (a) Laverty *et al.* (2015b) and (b) Ricciardi & Cohen (2007).

Fig. S3. Method 2 eqn 4 regression plots for (a) Laverty *et al.* (2015b) and (b) Ricciardi & Cohen (2007).

Fig. S4. Method 1 eqn 4 regression plots for (a) Laverty *et al.* (2015b) and (b) Ricciardi & Cohen (2007).

Table S1. Invader/native and invader/invader comparisons of Functional Responses, Abundances (or biomass) and "Relative Impact Potential" (RIP).

Table S2. All other combinations of Ecologial Impact Score against Relative Impact Potential (RIP). M=Method 1 or 2; E=eqns 4 or 5 - see Table S1 and main text.

Table S3. Regressions calculated from Table 1 and Table S2, see Figures 2a and b, Figures S2–S4.

Appendix S1. R Script: Relative Impact Potential (RIP) Calculation.

Appendix S2. Description of the different methods and equations used in Tables S2 and S3.

Movie S1. Invasive alien species and their ecological impacts are predictable after all!

